Forest processes from stands to landscapes: exploring model forecast uncertainties using cross-scale model comparison

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Abstract: Forest management practices conducted primarily at the stand scale result in simplified forests with regeneration problems and low structural and biological diversity. Landscape models have been used to help design management strategies to address these problems. However, there remains a great deal of uncertainty that the actual management practices result in the desired sustainable landscape structure. To investigate our ability to meet sustainable forest management goals across scales, we assessed how two models of forest dynamics, a scaled-up individual-tree model and a landscape model, simulate forest dynamics under three types of harvesting regimes: clearcut, gap, and uniform thinning. Althougth 50–100 year forecasts predicted average successional patterns that differed by less than 20% between models, understory dynamics of the landscape model were simplified relative to the scaled-up tree model, whereas successional patterns of the scaled-up tree model deviated from empirical studies on the driest and wettest landtypes. The scale dependencies of both models revealed important weaknesses when the models were used alone; however, when used together, they could provide a heuristic method that could improve our ability to design sustainable forest management practices.

Résumé : Les pratiques d'aménagement forestier qui sont surtout appliquées à l'échelle du peuplement entraînent une simplification de la forêt et engendrent des problèmes de régénération ainsi qu'une faible diversité structurale et biologique. Des modèles de paysage ont été utilisés pour aider à élaborer des stratégies qui s'attaquent à ces problèmes. Cependant, beaucoup d'incertitude persiste quant à savoir si les pratiques actuelles d'aménagement produisent une structure vraiment durable du paysage. Dans le but d'examiner notre capacité à atteindre les objectifs de l'aménagement forestier durable peu importe l'échelle, nous avons évalué de quelle façon deux modèles de dynamique forestière, un modèle élargi d'arbre individuel et un modèle de paysage, simulent la dynamique de la forêt soumise à trois régimes de coupe : rase, par trouées et éclaircie uniforme. Même si les prévisions sur 50 à 100 ans produisaient des patrons de succession moyens qui différaient par moins de 20 % selon le modèle, la dynamique de sous-bois du modèle de paysage était simplifiée relativement au modèle élargi d'arbre individuel, tandis que les patrons de succession du modèle élargi d'arbre individuel déviaient des études empiriques sur les stations les plus sèches et les plus humides. Le fait que les deux modèles soient dépendants de l'échelle fait ressortir d'importantes faiblesses lorsqu'ils sont utilisés séparément. Par contre, utilisés ensemble ils pourraient fournir une méthode heuristique capable d'améliorer notre capacité à concevoir des pratiques d'aménagement forestier durable.

[Traduit par la Rédaction]

Introduction

Spatial and temporal heterogeneity of species composition and structure are key components for maintaining resiliency of forest ecosystems (Wiens 1989; Forman 1995; Puettmann et al. 2008). However, with its priority on timber extraction, 20th century forest management practices have reduced landscape heterogeneity according to several metrics, including forest age class (Bergeron et al. 1999) and spatial structure (Hunter 1990; Cissel et al. 1999). Forest management

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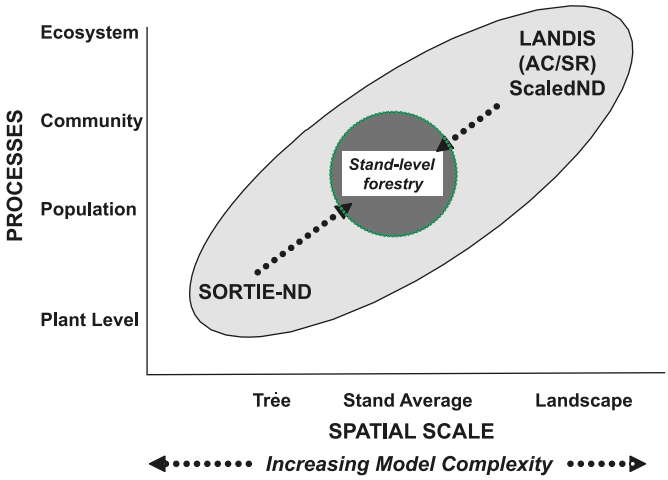
practices are increasingly driven by concerns for multiple uses that include cultural, aesthetic, and socioeconomic values as well as timber yields while retaining natural variability and forest ecosystem function (e.g., Burton et al. 2003; Puettmann et al. 2008). Determining which management strategies will most likely result in desired future species compositions and structures with minimal loss of future options presents serious scientific, societal, and technical challenges.

Concerns for multiple uses of forest resources span scales from trees to landscapes. Analyzing the effects of different uses are typically treated separately, which increases the risk that forest structure becomes overly simplified at one or more scales because what may be an excellent strategy to meet an objective at one scale may conflict with goals at other scales (Kneeshaw et al. 2000; Tittler et al. 2001; Coates et al. 2003). For example, single- or group-tree removal (i.e., selection cut systems) is designed to maintain diameter distribution and structural variability at the stand scale, but repetition across the landscape leads to homogenization of forest structure at larger spatial scales. To make effective forest management decisions and improve our confidence that the sum of all the operational decisions will meet long-term multiscale landscape objectives, it is critically important to reconcile planning and practice at various spatial scales.

Attempts to forecast ecosystem dynamics at broad spatial scales usually scale up the mean behavior of fine-scale processes by extrapolation (Fall et al. 2004; Mladenoff 2004; Urban 2005). These extrapolations are unreliable, however, as errors in estimates of the mean fine-scale behavior propagate to the broader scale and introduce spatial and temporal bias (Rastetter et al. 1992; Li and Wu 2006). Furthermore, spatial processes affected by tree neighborhoods in forested systems, such as fine-scale spatial characteristics of harvesting practices (Coates et al. 2003) and competitive relationships among species (Canham et al. 2006; Papaik and Canham 2006), are those that are least amenable to simple extrapolation to the landscape scale (Peters et al. 2004).

Landscape models simplify how they represent fine-scale processes to focus on broader-scale phenomena, such as disturbance (Peterson 2002), and are often used to support strategic landscape conservation and management planning. Because many fine-scale processes play important roles in conservation and sustainable management (Franklin 1993; Greene et al. 2002), however, we need to improve our confidence that stand-scale management practices will fulfill landscape planning objectives. New ecosystem- or resilience-based forest management requires adding appropriate complexity at both fine and broad spatial scales (Fig. 1) and ascertaining that management actions taken at the local scale fulfill management objectives made for the landscape scale. We propose an approach designed to simultaneously explore forest dynamics in managed forests simulated at both neighborhood and landscape scales. The approach gives managers a tool to investigate alternative scenarios at multiple scales in a consistent framework and improve our understanding of how current forest management practices impact future options. However, in the absence of fine-scale data collected over large spatial scales and long temporal periods, this approach cannot be used to decide which model is better, nor

Fig. 1. Conceptual diagram illustrating the spatial disconnection between fine-scale models and landscape models and 20th century forest practices that relied on highly simplified models that ignored important fine-scale and landscape-scale processes that resulted in simplifiied forests more susceptible to disturbance and less suitable habitat for supporting biodiversity.



can one model be used to validate or invalidate results from the other (Rastetter 2003).

We use SORTIE-ND for modeling neighborhood tree dynamics and a model we call AC/SR, for age cohort/shade tolerance rank, that was derived from LANDIS v3.6 for modeling landscape dynamics. SORTIE-ND is a version of the spatially explicit, individual-tree model SORTIE (Pacala et al. 1996? Coates et al. 2003) that extrapolates from fine-scale and short-term interactions among individual trees to large-scale and long-term dynamics of forest communities. LANDIS is a landscape model consisting of landscape-level processes of disturbance and seed dispersal as well as stand-level processes of regeneration, growth, mortality, and seed production (Mladenoff et al. 1996; Mladenoff and He 1999). The choice of these two well-respected models was dictated by the needs of the project within which this work is embedded (Sturtevant et al. 2007), but any two corresponding models of forest dynamics could be used. The models were evaluated using a common meta-modeling platform, SELES (Spatially Explicit Landscape Event Simulator) (Fall and Fall 2001). Meta-modeling is increasingly being used in numerous management and conservation contexts (e.g., Dale et al. 2008; O'Flaherty et al. 2008; Côté et al. 2010). We evaluate the results under the premise that such a comparison is valid if (*i*) the differences in scale between the models can be reconciled so that models are compared at the same scale and (*ii*) output data chosen for comparison fall within the intersection of the state-spaces of the models. Both models have been shown to meet "expectation" in these forests and found sufficient for use in forest management (Pennanen et al. 2004; Poulin et al. 2008). In this paper, we show how models can meet expectation, yet can disagree in important ways. This disagreement highlights otherwise hidden uncertainties in our forecasts. Our aim is to gain insight into our ability to meet both fine- and coarse-scale sustainable forest management objectives and to assist forest managers in balancing an increasingly diverse set of resource objectives.

Methods

Study area

The Lake Duparquet Research and Teaching Forest (FERLD) is in the Boreal Shield Ecozone (approximately 48°30′N, 79°22′W) in the southern region of the Great Clay Belt in western Quebec, Canada. The study area is approximately 16 000 ha of which 11 061 ha are classified into five forested landtypes (Fig. 2): moist, moist-clay, mesic, mesic-clay, and dryish on coarse soils. Species composition is characteristic of the eastern boreal mixedwood (Bergeron 2000; Chen and Popadiouk 2002).

Scaling framework

Modeling neighborhood dynamics (ND)

SORTIE-ND is a stochastic, spatially explicit, individual-tree, neighborhood-scale model that simulates stand development as an outcome of interactions among trees using empirically supported mechanistic relationships in four basic submodels: seedling recruitment, light availability, growth, and mortality (Pacala et al. 1996) plus submodels for natural disturbance and harvest (Canham et al. 2001; Coates et al. 2003). The harvest submodel can simulate any type of silvicultural strategy that removes or retains trees by species, size, and location. SORTIE-ND has been parameterized for six of the principle tree species in this region (Poulin et al. 2008): trembling aspen (*Populus tremuloides* Michx.), white birch (*Betula papyrifera* Marsh.), jack pine (*Pinus banksiana* Lamb.), white spruce (*Picea glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.), and eastern white-cedar (*Thuja occidentalis* L.). We used SORTIE-ND to generate 300 succession trajectories on 4 ha simulated stands initialized by a range of potential post-disturbance conditions (five variants) on five different forested landtypes, each with three harvest regimes and four alternative in-seeding assumptions used as surrogates for long-distance dispersal (LDD) scenarios (Supplementary Appendix A[3]) in which eastern white-cedar immigration started at 50, 100, and 150 years and never on the four landtypes that eastern white-cedar are able to establish.

Scaling ND to the landscape (scaledND)

The results of all 300 simulations were collated into a single look-up table (LUT), indexed by landtype, initial stand condition, stand age, and harvest regime to form a database for the landscape scale raster-based model (scaledND) that we implemented in SELES. The LUT specifies the number of stems per hectare and basal area by species for seedlings (trees <1.3 m tall), saplings (nonseedlings <10 cm DBH), and adults (trees >10 cm DBH) in 5 year time steps. The trajectory and initial conditions for each cell are determined from inventory data at 1 ha resolution used in Pennanen et al. (2004). The LUT is searched for the closest stand conditions to the inventory data, and the cell is populated with these data. Subsequent dynamics follow along the trajectory from that point. ScaledND succession proceeds in each cell according to the SORTIE-ND forecasts for that trajectory until a disturbance (in our case a harvest) occurs. When a harvest occurs, scaledND searches the LUT for the trajectory with the closest post-disturbance conditions. This may be earlier in the same trajectory or in an entirely different trajectory at any time in its history. If there are two different entries in the LUT that describe the post-harvest state, the density and basal area are taken as averages and follows the average of those two trajectories until another disturbance occurs. Hence, scaledND selects the successional state for a given cell from a distribution representing the range of variability expected given the environment, disturbance history, LDD in-seeding assumptions, and stand age. ScaledND is thus an approach for extrapolating (i.e., scaling) processes occurring at the individual-tree neighborhood using simulations of SORTIE-ND up to the landscape that allows us to compare the forecasts with the more traditional way of extrapolating used in a landscape model.

Landscape modeling

Our approach for implementing landscape-scale dynamics, called AC/SR, is based on Pennanen et al. (2004) whereby we implemented in SELES the core components of LANDIS v3.6 for their study of landscape forest dynamics in the same forests for which SORTIE-ND was parameterized in northern Quebec. Using SELES to implement AC/SR, rather than LANDIS directly, as the platform for comparing the two approaches allowed us to precisely match initial landscape conditions, specify identical harvesting schedules for each cell in each model, isolate the effects of the structural differences between the two models on forecasts of forest dynamics, and manage outputs to support the comparison.

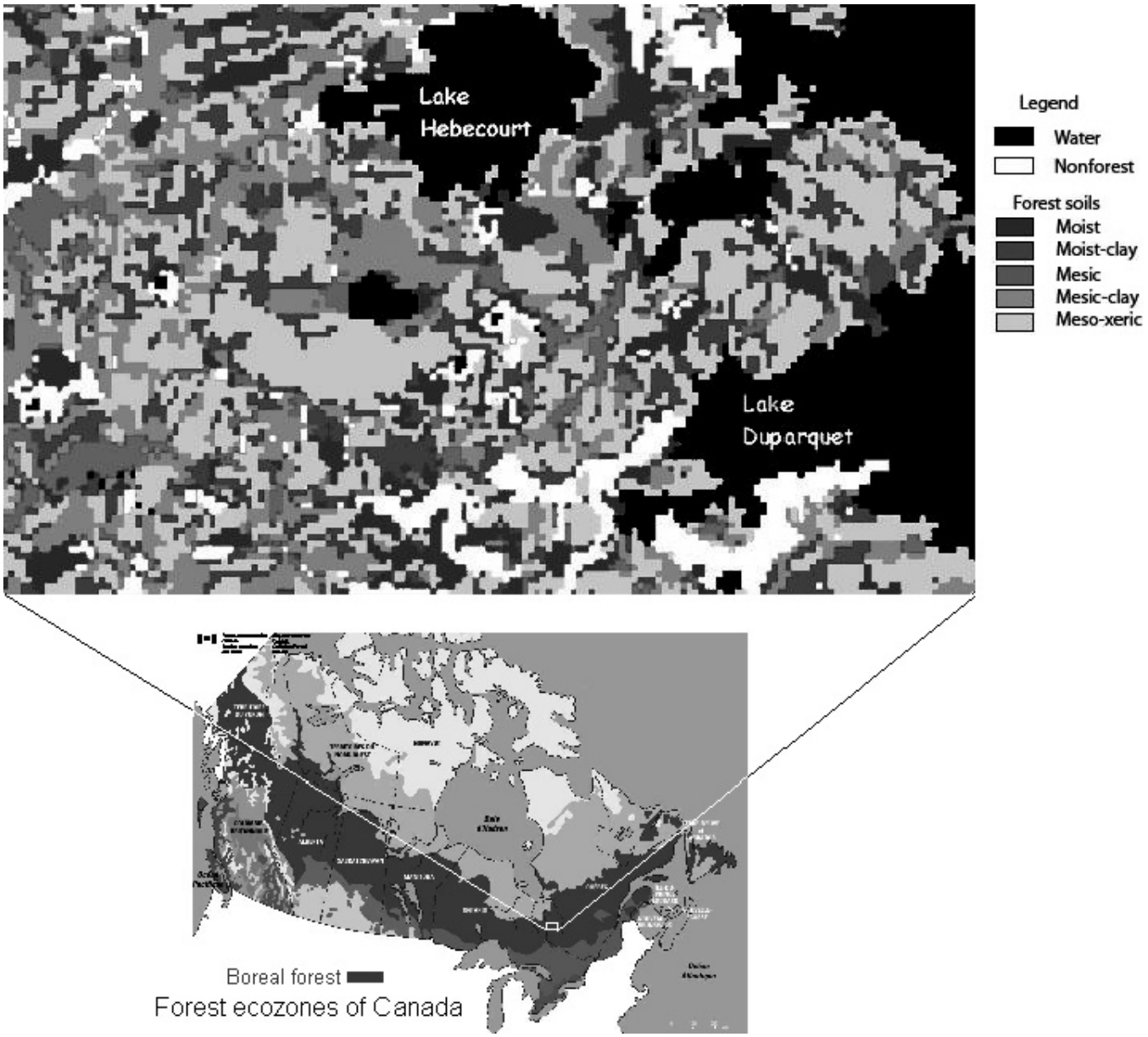
AC/SR dynamics are rule-based behaviors that affect the presence or absence of tree species in 10 year age cohorts within homogeneous raster cells (resolution 0.16 ha) (Supplementary Appendix B, Table B1[3]). At each time step, surviving cohorts age, young cohorts establish (according to shade tolerance rank rules, availability of seed source, and landtype specific establishment probability), and some cohorts die as a result of senescence or disturbance. Landtypes are defined as groups of cells that are assumed to be homogeneous with respect to their environmental characteristics (e.g., microclimate, soil type, and (or) topographic position). Mature cohorts are defined as those containing trees old enough to disperse propagules, and seeding is modeled as a spatial process among cells, with seed availability dependent on species-specific distance to cells with mature cohorts.

Model comparison

Three key differences between AC/SR and scaledND are (*i*) AC/SR simulates variation in local dynamics across landtypes with parameters that determine the seed dispersal and probability of a sapling cohort establishing on each of five landtypes, whereas SORTIE-ND is parameterized for mesic sites only but was adapted to the other four landtypes for the purposes of this study by adjusting the recruitment parameter analogously to AC/SR (Supplementary Appendix B, Table B2[3]), (*ii*) scaledND summarizes local variation in dynamics as a result of modeled interactions among individual trees, whereas AC/SR ignores within-cell spatial processes and specifies succession using strict rules based on species rankings of shade tolerance and probabilities of establish-

[3] Supplementary material is available on the journal Web site (http://cjfr.nrc.ca).

Fig. 2. We gridded our 16 000 ha study region, located in the Lake Duparquet Research and Teaching Forest, into 1 ha cells, each of which is classified as one of five forested or two nonforested landtypes that determine the regeneration dynamics of trees. Total forest area of our study is 11 061 ha.



ment, and (3) scaledND has no mechanism to determine LDD in-seeding based on information regarding the presence of a species in a nearby cell, whereas LDD is explicitly simulated in AC/SR using empirically calibrated dispersal parameters determined in Pennanen et al. (2004) (shown in Supplementary Appendix B, Table B2[3]).

AC/SR represents stand-scale conditions as a grid of cells containing information on the presence of age cohorts of each species, while scaledND tracks the density and basal area per hectare of each species by life stage (seedling, sapling, and adult). In scaledND, adults (trees capable of generating seeds and reproducing) are the trees from SORTIE-ND simulations with >10 cm DBH; in AC/SR, a cohort of trees are adults (mature) if they exceed a specified age (Supplementary Appendix B, Table B1[3]). To reconcile the different outputs from these approaches and facilitate comparing results, we collapsed the information generated by scaledND to the presence of any saplings and the presence of adults if the basal area is >1 m^2/ha. Our simulation test setup is designed to explore the consequences of these differences in model structure.

Simulation experimental design

Initial conditions and nondisturbance succession

Existing stand age and land cover type data were derived from inventory data at 1 ha resolution (Pennanen et al. 2004) and were used as a basis for the initial landscape conditions for both scaledND and AC/SR as explained above. There were five forested cover types that were specified ac-

cording to coarse soil characteristics and moisture retention ability (moist, moist-clay, mesic, mesic-clay, and dryish) (Pennanen et al. 2004). Cover type resolution was aggregated to 4 ha for both AC/SR and scaledND. However, to match the spatial pattern of all harvest scenarios, we defined twenty-five 0.16 ha AC/SR harvest cells for each 4 ha cover type cell (Fig. 3). Initial conditions were determined for scaledND as explained above, and then the scaledND values for each cell were used to determine the equivalent starting conditions (i.e., species cohorts) for AC/SR. We created the cohort structure for each species in the cell that best approximated the presence of seedlings, saplings, and (or) adults in the LUT. This approach is designed to handle any number of landtypes, initial stand conditions, harvest regimes, disturbance types, and LDD scenarios.

Harvest scenarios

We developed a simple harvest pre-processor using SELES that selects the same set of contiguous groups of cells (i.e., cut blocks) to harvest in scaledND as in AC/SR for any individual scenario. Thus, we control minimum harvest re-entry age (60 years), block size targets (mean of 20 ha), and rotation interval (80 years) identically for each approach. This time series of harvest patches is used as input to both AC/SR and scaledND to ensure that harvest disturbances are as equivalent as possible between models. We compared the results of the two models using the nonharvest scenario described above and three harvest scenarios: (1) clearcut, (2) 60% gap cut, and (3) 60% uniform thinning. There were 10 replicates of each scenario.

Simulated clearcuts reset scaledND succession in the cut cells to initial stand conditions for that trajectory. A clearcut in AC/SR removes all cohorts from all cells in a cutblock and regeneration proceeds according to dispersal dynamics from adjacent cells. A gap cut in scaledND switches to the SORTIE-ND gap cut trajectory that most closely matches stand conditions before the harvest and follows that trajectory immediately after the cut; in SORTIE-ND, all mature trees are removed from the central 60% of the 4 ha plot. A gap cut in AC/SR removes all mature cohorts from 60% of the 0.16 ha cells in each 4 ha landtype cell in each cutblock (Fig. 3). There are two alternate thinning regimes in AC/SR that correspond to the 60% thinning regime from SORTIE-ND: (*i*) a randomly chosen 60% of mature cohorts were removed from each cell and (*ii*) the oldest 60% of mature cohorts were removed. Decimal remainders were removed probabilistically. For example, if there are four mature cohorts, two are removed (either randomly or the oldest two). The next cohort has a 40% chance of being removed ($0.6 \times 4 = >2.4$ cohorts should be removed). Full details on the harvest regimes can be found in Supplementary Appendix A.[3]

Results

We present our primary results as the dfferences between the two model forecasts in each scenario to emphasize the uncertainties involved by using both fine- and large-scale models to support sustainable forest management objectives. Model-specific results of all of our scenarios are given in Supplementary Appendix B, Figs. B2–B5[3].

Stand scale (SORTIE-ND only)

Variation within landtypes was created by the interactions among individual trees from a relatively modest factor of two differences in the initial relative abundances of saplings 130–135 cm tall (Supplementary Appendix B, Table B2[3]). This generated considerable variation in relative species abundance of trees >10 cm DBH on all landtypes for the first 200 years, after which, in the absence of disturbance, white spruce and balsam fir dominate on all but the dryish sites, where balsam fir and white birch dominate (Fig. 4). On each landtype, in the absence of disturbance, eastern white-cedar begins to dominate stands starting around 300 years after stand initiation, which is generally consistent with historical data that suggest that eastern white-cedar was dominant in a number of places where fire cycles were long (Bergeron 2000).

There is also considerable variation in succession among the different landtypes, despite relatively modest differences in recruitment (Supplementary Appendix B, Table B1[3]). On moist sites, white spruce and white birch dominate early followed by white spruce dominance; on moist-clay and mesic sites, white birch and trembling aspen dominate early followed by white spruce and balsam fir on moist-clay and with balsam fir becoming more dominant on mesic sites; mesic-clay sites start with a mix of white birch, trembling aspen, and white spruce that transitions to white spruce and balsam fir after about 100 years and then to dominance by balsam fir; dryish sites start with a similar mix but succeed to white birch and balsam fir after about 150 years.

Landscape scale (scaledND and AC/SR models)

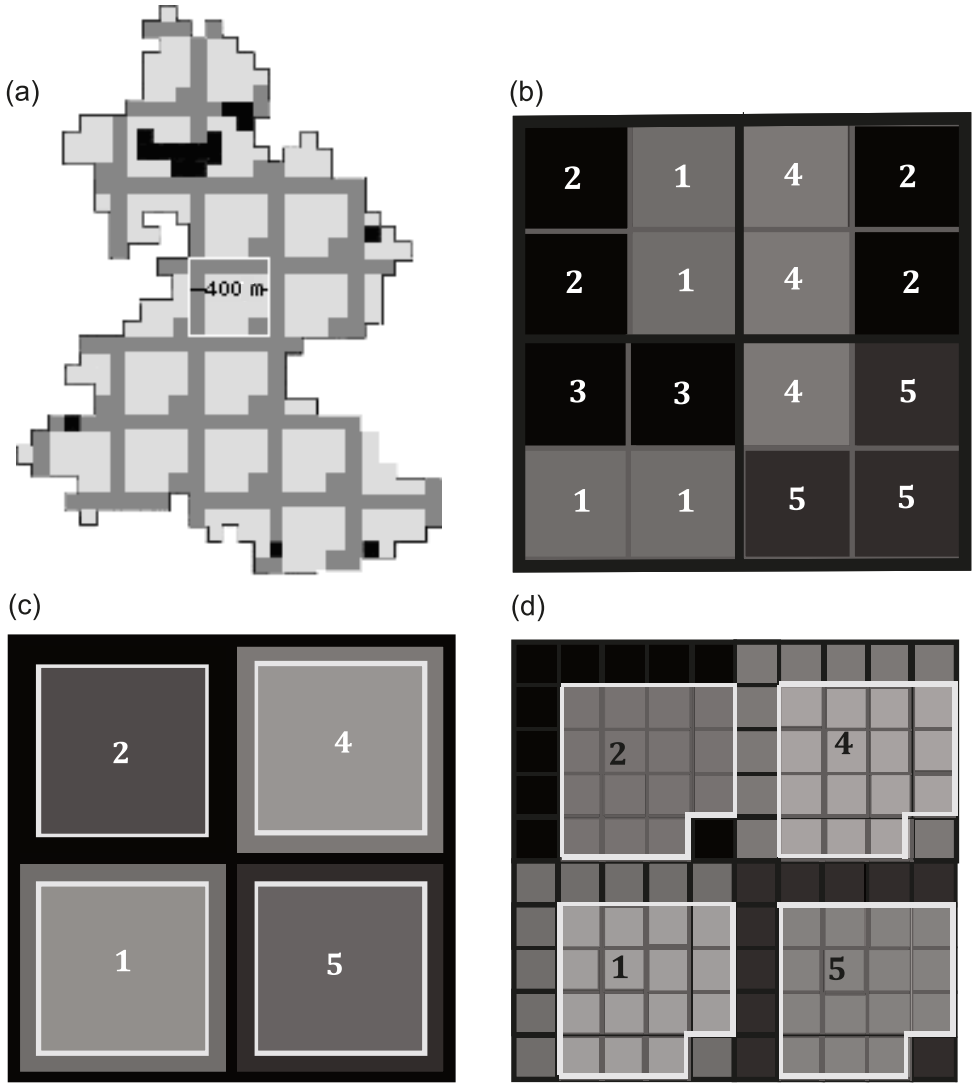
Both models' successional dynamics are broadly similar and follow well-known shade tolerance patterns, which in the absence of disturbance predict that more shade-tolerant species increase their landscape presence over time and persist longer than less shade-tolerant species. We ran 10 replicates of each model for each of our scenarios. Both models include stochasiticity but still have very low variation in forecasts of average landscape dynamics (Table 1). Either model used alone may give users a sense that there is little uncertainty in the forecasted outcomes. However, while both models predict very similar relative presence of balsam fir and jack pine, the most and least shade-tolerant species, respectively, after the first 20–30 years in our simulations (Figs. 4 and 5), there is a great deal of uncertainty (as expressed by the difference in predicted presence) among the three midtolerant species (trembling aspen, white birch, and white spruce) (Table 2).

No-harvest scenario

In the absence of harvest, there is no general pattern relative to shade tolerance ranking in which one of the two models predicts greater or lesser presence of mature trees of these species in the landscape over time (Fig. 5), but there are discernable shade tolerance patterns in model predictions that change with time since stand initiation: the first 20 years (initiation period), between 20 and 100 years (harvest cycle period), and after 100 years (mature landscape period).

During the initiation period, scaledND initially predicts greater abundance of the two most shade-tolerant and less abundance of the three shade-intolerant species, although

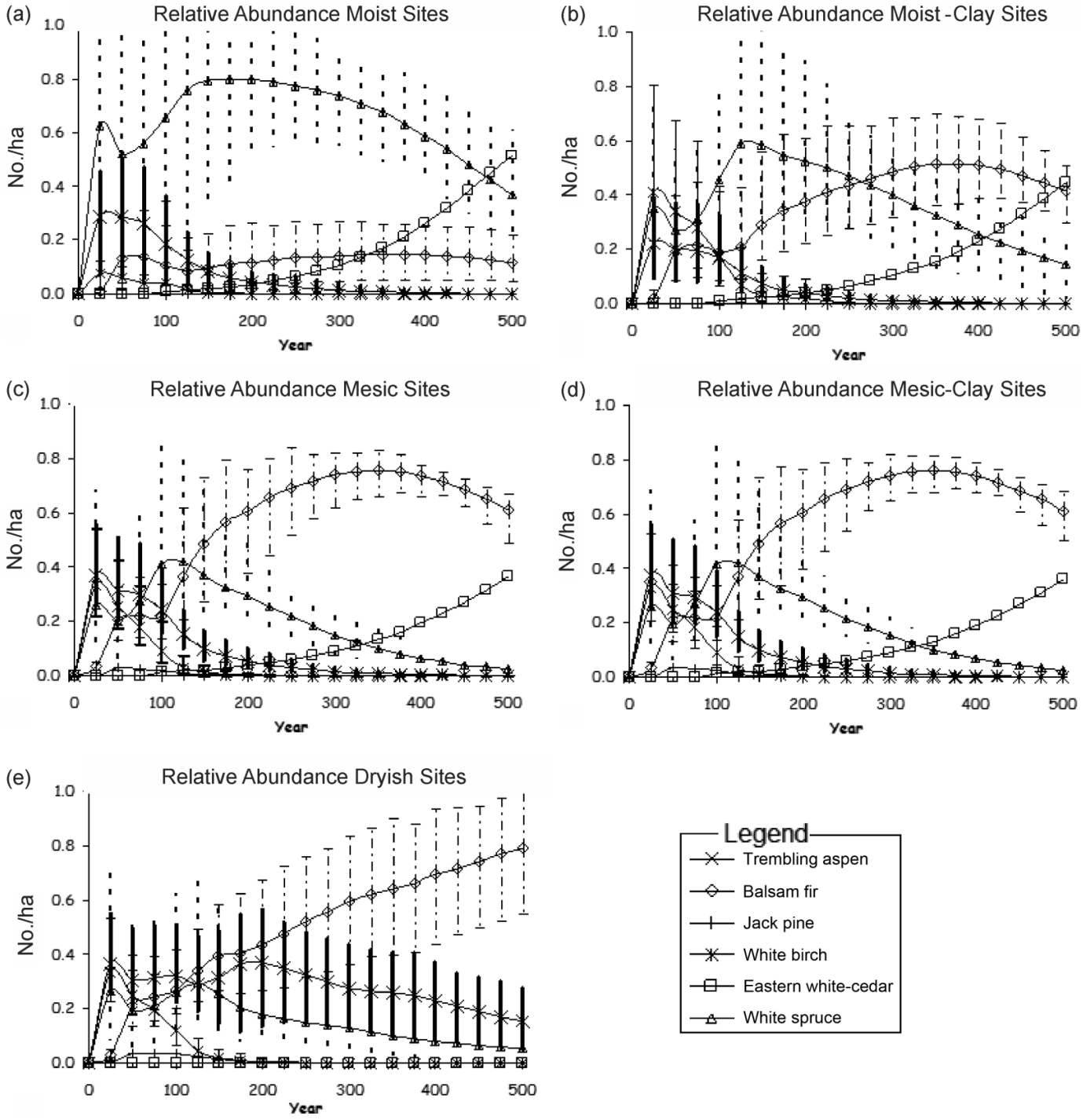
Fig. 3. Spatial synchronization of scales between the forest classification map and harvests in the two models. (*a*) The large irregular area is a harvest unit defined identically in the two models in the harvest pre-processing step. The black areas are nonforest landtypes and are ignored if they fall within a cutblock. The gap-harvested cells in AC/SR are light grey, while nonharvested cells are dark gray and correspond to the details in Fig. 3*d*. The white bordered square area in the center of the harvest unit represents the 16 ha area (400 m × 400 m) detailed in Figs. 3*b*–3*d*. (*b*) Original 1 ha forest landtype cells (grey borders). Numbered shades of grey represent different forest landtypes. Black borders define minimum scaledND harvest cells (4 ha) that match SORTIE-ND plot resolution to allow closest spatial approximation of harvesting in the two approaches. (*c*) Four hectare scaledND cells (black borders corresponding to those in Fig. 3*b*) with 60% gap cut area (bordered in white) from which individual trees were harvested in the SORTIE-ND simulations. Each 4 ha cell is classified as one forest type. (*d*) AC/SR succession is defined by 40 m × 40m cells (black borders) with gap cut cells enclosed within white borders. Since 25 cells make up one 4 ha harvest cell unit, 15 (60%) of the cells are harvested. The twenty-five 40 m cells corresponding to one 4 ha harvest cell unit are assigned the same forest type as scaledND.



these differences are less than 20%. During the harvest cycle period, both models forecast equivalent presence of all species except eastern white-cedar (Fig. 5). However, as time goes by, forecasts of trembling aspen dynamics diverge. The presence of trembling aspen in AC/SR slowly increases compared with scaledND to approximately 18% until an abrupt switchover occurs at year 130 when scaledND predicts 75% greater presence than AC/SR. Jack pine, white birch, and white spruce predictions experience similar abrupt changes at years 150, 170, and 280, respectively, corresponding roughly to AC/SR species longevity parameters (Supplementary Appendix B, Table B1[3]). The differences in predicted presence of the two most shade-intolerant species, trembling aspen and jack pine, slowly decrease until about year 250, after which there is no difference in jack pine abundance (the species disappears from the landscape) and AC/SR predicts trembling aspen to be slightly more abundant than scaledND.

Regeneration differs greatly between the two models and explains in part the differences in mature trees after approximately 100 years (Fig. 5*b*). During the initiation period, AC/SR regeneration is greater than scaledND for all

Fig. 4. Stand-scale variation among the SORTIE-ND runs. Variation comes from two sources: variation in recruitment among landtypes and variation in initial stand conditions within landtypes. Within-landtype variation is illustrated by the error bars that show the minimum and maximum relative abundances of four of our species (trembling aspen, white birch, white spruce, and balsam fir) on each of the five landtypes: (*a*) poorly drained landtype, (*b*) moist-clay landtype, (*c*) mesic landtype, (*d*) mesic-clay landtype, and (*e*) well-drained landtype. Variation in trembling aspen and white birch is shown using thin and thick solid lines, respectively, with trembling aspen capped and white birch uncapped. Balsam fir and white spruce variation is highlighted by thin dash-dotted and thick dashed lines that are capped and uncapped, respectively.



species other than balsam fir. This changes after the initiation period when scaledND predicts greater presence of regeneration of all but one species, eastern white-cedar. Differences in regeneration are due to the absence in AC/SR of regeneration of any species other than the two most shade-tolerant species after the first 40 years with a minor exception between years 260 and 300 for white spruce and trembling aspen.

Table 1. Structural components of SORTIE-ND, scaledND, and AC/SR compared in this study.

Characteristic	SORTIE	scaledND	AC/SR
Trees	Individual DBH, *x*,*y* coordinates; species-specific allometric functions	Implicit density per hectare for seedlings; basal area, density per hectare for saplings and adults of each species for each 5 year time step	5 year age cohorts: first cohort seedlings, subsequent cohorts saplings up to age of maturity, remaining cohorts adults
Local dispersal, regeneration	Spatially explicity, species-specific fecundity and seedbed establishment	Implicit	Presence of seeds: vegetative, seeding from current mature cohorts Establishment of seeds: (*i*) shade tolerance rules, (*ii*) if tolerance rules allow species-specific probability of establishment
Long-distance dispersal	Bootstrap step 1: constant seed rain input based on hypothesized basal area within dispersal distance Bootstrap steps >1: seed rain determined by expected basal area of adult trees within long-distance dispersal distance of stand as estimated by previous landscape iteration	Implicit	Seeding based on
Sensitivity to landtype	Fecundity a function of relative probability of establishment on different landtypes	Implicit	If tolerance rules allow establishment, then species-specific probability of establishment
Growth	Species-specific function of available whole-season light	Implicit	Simple aging of cohorts
Mortality	Probabilistic function of growth	Implicit	None until 80% of expected lifetime,then linear increasing probability of mortality until 100% when cohort is removed

Harvest scenarios

Clearcut

Differences in the predicted presence of mature trees in the clearcut harvest scenario are simpler but still follow only a weak shade tolerance pattern. The two most shade-tolerant species (balsam fir and eastern white-cedar) and the least shade-tolerant species (jack pine) have the greatest differences in predicted presence. ScaledND forecasts greater presence of jack pine than AC/SR, and AC/SR forecasts greater presence of balsam fir and eastern white-cedar. This relationship does not hold for the three midtolerant species, however. While the two models' predictions are within 20% throughout, scaledND predictions of white spruce exceed AC/SR, whereas AC/SR predictions of the two less shade-tolerant species are greater. In absolute terms, both models' predictions stabilize early in the simulations (scaledND at 30 years and AC/SR at approximately 200 years).

There are much greater differences in forecasts of regeneration between the models than in mature tree dynamics (Fig. 6*e*). There is a clear relationship between the difference in the predictions and shade tolerance characteristics. AC/SR predicts greater presence of shade-tolerant species and scaledND predicts greater presence of shade-intolerant species. The lone exception to this is for shade-tolerant balsam fir regeneration, which is predicted to be virtually ubiquitous by both models.

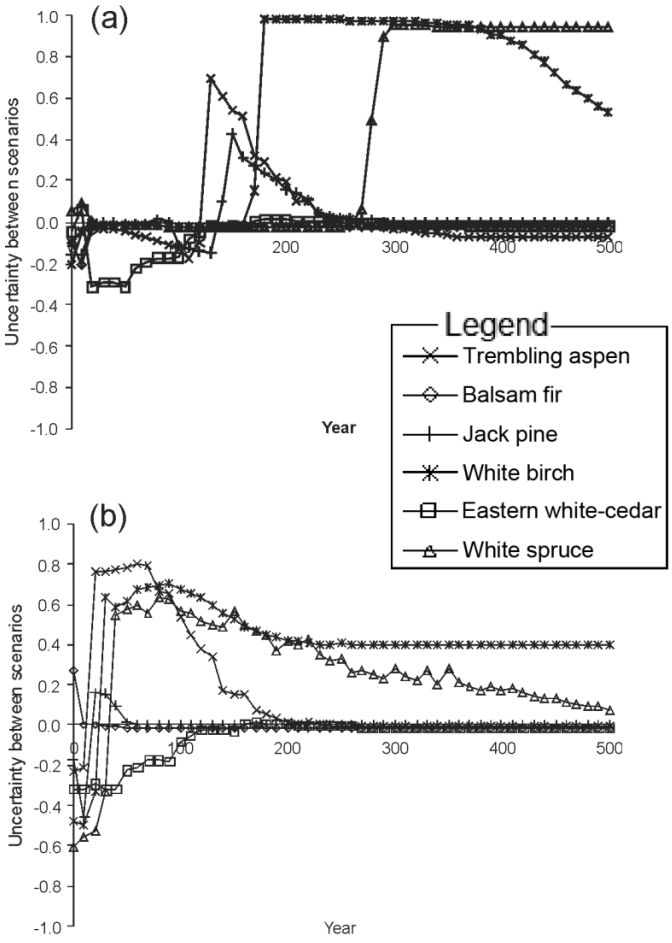
Gap cut

With the exception of trembling aspen, gap cut predictions of mature tree presence were more similar between the two models than other scenarios. Both models predicted that balsam fir, white birch, and white spruce would be common in the landscape. The primary difference was trembling aspen. Both models predicted similar presence of trembling aspen for the first 130 years, with AC/SR predicting it to be slightly more common. After 130 years, trembling aspen presence drops from 100% to approximately 80% in AC/SR, after which it remains constant, but scaledND predicts that trembling aspen presence will slowly decrease to near zero after 500 years, resulting in great uncertainty between the two models' predictions of long-term trembling aspen presence in the landscape. As with the other scenarios, predictions of regeneration in the gap cut scenario differ more than mature tree predictions between the two models. Generally speaking, scaledND predicts greater regeneration of less shade-tolerant species than AC/SR with the exception of jack pine whose mature trees have dropped out of both landscapes by approximately 150 years.

Uniform thinning

There were two harvest strategies in AC/SR that approximated the scaledND thinning strategy. The first strategy removed 60% of the mature cohorts from harvested cells (Figs. 6*c* and 6*g*). The second removed the oldest 60% of mature cohorts (Figs. 6*d* and 6*h*). The difference is rather subtle and results in similar timing of the differences between the predictions but results in large differences in their magnitudes (Figs. 6*c* and 6*d*). Generally speaking, the first

Fig. 5. Difference of the average of 10 replicate runs in presence–absence per 4 ha of mature trees between the two models in the absence of harvest (positive values indicate higher values in scaledND and negative values indicate higher values in AC/SR). (*a*) Mature trees; (*b*) sapling regeneration.



AC/SR strategy more closely approximates the scaledND regime. The differences in regeneration dynamics of both AC/SR regimes from scaledND are very large (Figs. 6*g* and 6*h*), but the differences between the two AC/SR thinning regimes are subtle. Only white spruce and white birch differ noticeably, with the second AC/SR regime predicting their regeneration to be less common in the landscape.

Discussion

The goal of this study is to explore some of the uncertainties implied by using fine-scale models to help implement harvest prescriptions while simultaneously attempting to fulfill landscape objectives defined in part using landscape models. Whenever possible, model uncertainty should be assessed by comparing forecasts against data collected independently. For situations where data cannot be obtained (e.g., long-term forest change, climate change), an alternative approach is to use forecasts of different models that structurally differ (Rastetter 2003). In addition to how they model succession, our two models differ in their spatial dynamics. In AC/SR, within-cell dynamics are nonspatial but among-cell dynamics are spatial because post-harvest dynamics depend in part on stand structure and composition in nonharvested cells around the cutblock. In scaledND, within-cell dynamics are spatial, capturing within-cell spatial interactions, but among-cell dynamics are nonspatial given that scaledND has no information about adjacent cells. We chose to compare these particular models because they had been parameterized for our region and already used to investigate consequences of various management activities (Pennanen et al. 2004; Poulin et al. 2008). Other models that represent stand dynamics or landscape dynamics in different ways could also be employed (e.g., Kimmins et al. 1999; Scheller et al. 2007; Purves et al. 2008).

Neighbourhood dynamics: difficulties with scaling up

The variation in succession within and among landtypes of the SORTIE-ND simulations follows the general pattern for boreal forests of the region (Bergeron 2000; Chen and Popadiouk 2002) and is a reasonable first approximation of the three most mesic of the five forest types of the range of succession found in the boreal mixedwoods considering the limitations of our test setup. On the dryish landtype, we expect to find higher relative abundances of white spruce and jack pine (Fig. 3*e*), as both balsam fir and white birch are known to require moisture for successful seedling establishment (McLaren and Janke 1996) and on the moist landtype (Fig. 3*a*), white spruce is usually not found in such high relative abundance as in our simulations (Bergeron 2000). These particular results are a consequence of (*i*) the relatively narrow range in initial stem densities within landtypes and (*ii*) the assumption that successional dynamics on different landtypes are controlled exclusively by differences in species establishment that we adopted from AC/SR. The narrow range within landtypes in initial stem densities gives us a more precise tool for assessing how fine-scale dynamics propagate to the landscape scale. Assuming that differences in successional dynamics among landtypes are solely controlled by differences in establishment was a necessary modeling simplification. In addition to recruitment, many ecosystem factors vary among landtypes (e.g., soil moisture, richness) that can change both absolute and relative growth, probability of mortality, and the relative competitive abilities among species (Canham et al. 2006; Papaik and Canham 2006). Thus, despite advances in scientific understanding of processes affecting forest change, there remain significant hurdles to forecasting fine-scale tree dynamics across broad areas (Mladenoff 2004; Gustafson et al. 2010). Our results confirm this perspective and suggest that to obtain a reliable model that forecasts species dynamics across landtypes, we must also account for the varying effects of soil properties on tree species growth and mortality and not just recruitment.

Landscape dynamics: evaluation and limitations

Our choice of the range of initial stand conditions in the SORTIE-ND simulations reduced the potential heterogeneity in forest dynamics possible for both landscape models. The restriction helps us focus on the consequences of the two different ways that the models represent succession in the context of harvest activities and improves our confidence that the methodologies of the two models generate landscape dynamics in a manner consistent with natural processes. Our

Table 2. Standard error among iterations in predicted presence of each species in the Lake Duparquet landscape.

	Regime									
	No harvest		Clearcut		Gap cut		Uniform cut		Uniform cut 2	
Species	Adult	Sapling	Adult	Sapling	Adult	Sapling	Adult	Sapling	Adult	Sapling
ScaledND										
Trembling aspen	0.002	0.002	0.001	0.006	0.003	0.003	0.003	0.003	—	—
Balsam fir	0.001	0.001	0.001	0.001	0.000	0.000	0.001	0.001	—	—
Jack pine	0.002	0.001	0.004	0.005	0.002	0.001	0.002	0.001	—	—
White birch	0.002	0.002	0.001	0.004	0.001	0.003	0.002	0.003	—	—
Eastern white-cedar	0.003	0.003	0.002	0.002	0.003	0.003	0.003	0.003	—	—
White spruce	0.001	0.002	0.001	0.005	0.001	0.003	0.001	0.004	—	—
AC/SR										
Trembling aspen	0.000	0.000	0.001	0.000	0.001	0.003	0.007	0.003	0.008	0.003
Balsam fir	0.000	0.003	0.004	0.005	0.003	0.004	0.003	0.004	0.001	0.004
Jack pine	0.001	0.000	0.001	0.000	0.001	0.001	0.005	0.001	0.006	0.001
White birch	0.000	0.000	0.003	0.002	0.003	0.003	0.008	0.003	0.009	0.002
Eastern white-cedar	0.005	0.004	0.003	0.003	0.005	0.006	0.008	0.006	0.008	0.006
White spruce	0.000	0.000	0.003	0.002	0.003	0.005	0.009	0.005	0.010	0.004

Note: —, not applicable. Both models were run for 10 iterations with stochastic variation among runs. Variation between iterations was substantially lower than variation between models, indicating greater revealed uncertainty than what is inherent in either model. The two alternate uniform thinning strategies for AC/SR differed in their selection of which mature cohorts to remove. In "uniform cut", 60% of mature cohorts were removed from each cell; in "uniform cut 2", the oldest 60% of mature cohorts in each cell was removed where decimal remainders were removed probabilistically. For example, if there are four mature cohorts, the oldest two are removed and the third oldest has a 40% chance of being removed (because $0.6 \times 4 = 2.4$ cohorts).

ability to compare these models experimentally helps us discern how the processes embodied in the models generate heterogeneity and determines to what degree they are appropriate for examining the types of questions in sustainable forest management. Having good estimates of both understory and overstory species composition is important in forecasting post-harvest dynamics because relative species abundance in post-disturbance stand conditions in boreal and temperate forests generally resemble relative species abundance in pre-disturbance conditions (Chen and Popadiouk 2002; Frelich 2002). The uncertainty (as expressed by the difference in predicted presence) among the three midtolerant species (trembling aspen, white birch, and white spruce) and several key differences between the two models in the timing of these patterns and understory regeneration dynamics could have important management consequences.

Effects of scale on assessing cross-model uncertainty

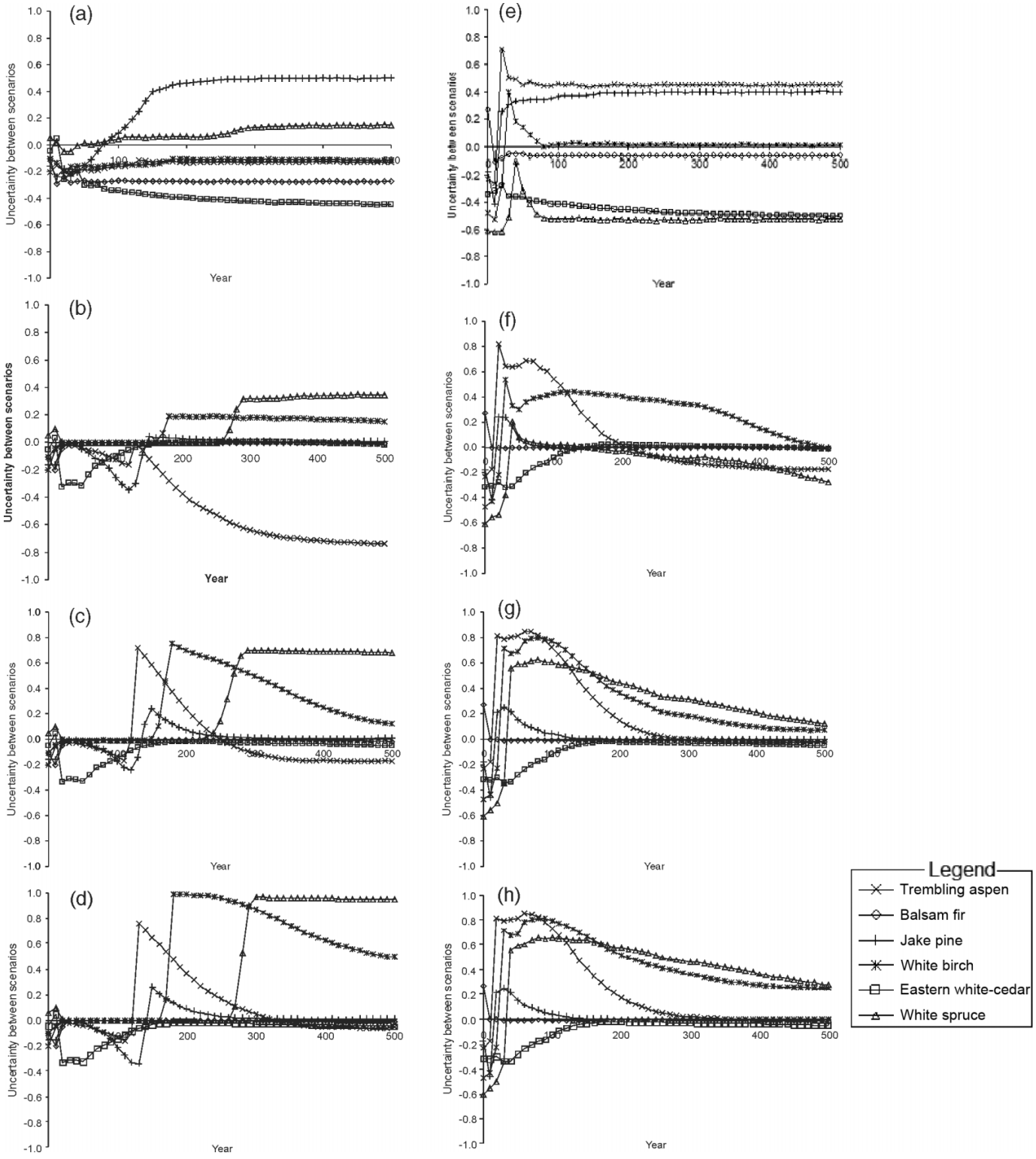
The objective of our scaling design was to eliminate differences in the results of the models due to scaling or spatial mismatches. We were able to match initial conditions and the spatial patterns of all of the harvest scenarios except gap cuts, which had a minor spatial mismatch (Figs. 3*c* and 3*d*). Forest landtype classification also suffered from a scaling issue. Because scaledND records the density and basal area per hectare over time of each species in the 4 ha simulated plot, we aggregated the land classification data for scaledND and matched AC/SR to that. We could have avoided this by subsetting the SORTIE-ND plot into four 1 ha cells and reported each cell's dynamics. This would have allowed us to use the full resolution of the landtype classification data. We recommend this in an actual implementation of this approach. However, it would still be necessary to choose a cell resolution for AC/SR somewhat less than 1 ha to maintain spatial synchrony of harvest scenarios. We also evaluated landscape dynamics on each of the five forested landtypes. Both models were sensitive to landtype and showed different forest dynamics on the different landtypes. It would be important in a management application for managers to consider this, but there were no new insights gained with respect to the goals of this study of highlighting uncertainties involved in multiscale forest management (results not shown).

Some implications for sustainable forest management

The general agreement between the AC/SR and scaledND projections of average adult tree dynamics (Fig. 5*a*) implies that we can be reasonably confident in the forecasts for our no-harvest scenarios at the landscape scale for a short period after stand initiation; however, differences in the projections of understory dynamics in that same timeframe (Fig. 5*b*) and the role of advance regeneration on subsequent succession have important limiting consequences to post-harvest dynamics and our ability to develop habitat risk indices (Morgan et al. 2007). Incorrectly accounting for these understory dynamics in our models could impact our ability to assess the sustainability of forest management actions, especially when forest management takes advantage of or is based on some expectations of advance regeneration, even if the landscape models capture mean mature tree dynamics adequately within the first 100 years.

Empirical data from the boreal mixedwoods region show that trembling aspen and balsam fir dominate after clearcuts and that succession mostly involves the shift from trembling aspen to balsam fir dominance (Kneeshaw and Bergeron 1998; Bergeron 2000). Because our initial neighborhood model stand conditions include all species (except eastern white-cedar) and because the range of initial stem densities is much less than found among stands, we expect scaledND to overstate actual white spruce importance and understate

Fig. 6. Difference of the average of 10 replicate runs in presence–absence per 4 ha of mature trees between the two models in each harvest scenario (positive values indicate higher values in scaledND and negative values indicate higher values in AC/SR). (*a*) Clear-cut harvest regime. (*b*) Gap harvest regime. (*c* and *d*) Two alternate AC/SR uniform thinning regimes: when a stand is thinned in scaledND, it is set to the closest post-harvest age in the corresponding SORTIE-ND thinning trajectory. There were two alternate analogous thinning strategies for AC/SR: (*c*) 60% of mature cohorts were removed from each cell and (*d*) the oldest 60% of mature cohorts in each cell were removed where decimal remainders were removed probabilistically. For example, in Fig. 6*c*, if there are four mature cohorts, the oldest two are removed and the third oldest has a 40% chance of being removed (because 0.6 × 4 = 2.4 cohorts). (*e–h*) Difference in sapling regeneration dynamics between the two models that correspond to harvests in Figs. 6*a*–6*d*, respectively.



actual trembling aspen importance in the clearcut harvest scenarios. Indeed in scaledND, white spruce, white birch, trembling aspen, and balsam fir are the most abundant species after clearcuts, whereas in AC/SR, balsam fir and white birch are the most abundant species (Fig. 4*a*). This is a consequence of a few processes that are missing from the simulations: advance regeneration of balsam fir (the abundance of which depends on the harvest methods), the practice of planting jack pine, and, in scaledND, vegetative reproduction by hardwood species. Hence, neither simulation model is completely consistent with current harvest methods and available regeneration strategies. Consequently, in these simulations, scaledND should be biased toward local preharvest conditions and AC/SR should be biased toward species with long-distance seeding advantages for the different harvest scenarios. Thus, our comparison reveals the importance of simulating the fullest likely range of stand conditions to better capture landscape dynamics and to highlight or identify processes missing or poorly accounted for in the models. By assessing these limitations, managers can evaluate the effects of these relative biases on the uncertainties revealed by comparing models.

The ability to better capture the effects of spatial variability in stand structure and species composition at multiple scales in management practices could permit the maintenance of key processes that in turn maintain biodiversity and productivity in managed landscapes (Franklin 1993). The complex needs of sustainable forest management and conservation push the limits of our models at both stand and landscape scales. It is commonly taught that all models are simplifications of nature and are designed with limited scopes. But, as management needs become more complex, trusted models are often extended to address the new needs without all of the extensive testing that is needed to fully validate the extended model. Landscape models add process detail at some risk of adding bias (Gustafson et al. 2010) and fine-scale models extrapolate processes with similar consequences (Urban 2005). Therefore, we are well served to develop efficient heuristic approaches that help estimate the limits more precisely. In this case, our approach helps us evaluate some limits for both the neighborhood and landscape models. For instance, the shortcomings of the SORTIE-ND results on the driest and wettest landtypes illustrate that the scope of its use can be stretched somewhat beyond the strictly mesic sites for which it was parameterized by adopting the approach used by AC/SR (i.e., scaling the recruitment parameter for the different landtypes). Likewise, the shortcomings of the AC/SR results illustrate that its scope, too, can be stretched somewhat in some circumstances to include partial disturbances within the timeframe of simulating management scenarios because of the importance of initial conditions, which a careful user takes pains to specify accurately.

Estimating the effects of management on biodiversity at different scales

The concordance of adult tree dynamics between the two models in the timeframe that is important to forest managers reinforces our confidence that the general, average forecasts of our models are likely reliable. However, the lack of understory response in AC/SR to variations in harvest of the forest canopy represents an important shortcoming with respect to managing diversity from a sustainable management perspective. Lack of LDD in scaledND is a corresponding issue that limits the accuracy of understory forecasts. Understory vegetation critically influences successional patterns, particularly following forest harvesting (Chen and Popadiouk 2002). Further, understory forest structure is a major component determining habitat quality for a variety of biodiversity values important in boreal and other forest biomes including songbirds (Simon et al. 2000; Fink et al. 2006), small mammals (Simon et al. 1998), and large mammals (Fisher and Wilkinson 2005). These are important ecosystem services that the public demand forest planners to consider. These different limitations of models designed to explore dynamics at different scales mean that it is particularly important to assess multiscale uncertainties when addressing biodiversity questions. The importance of model forecasts is all the more critical when we consider the importance of disturbance to boreal forests (Chen and Popadiouk 2002) and because emulating natural disturbance is considered an important strategic approach to sustainable management of our forest resources (Cissel et al. 1999). Therefore, to support sustainable forest management planning, our models need to be robust enough to capture a reasonable amount of the complexity and heterogeneity of forests at both stand and landscape scales. Otherwise, managers cannot have reasonable confidence that current management decisions made for one scale will provide the values and services demanded by society that span other scales.

Sustainable forest management planning is generally a hierarchically structured endeavor that starts with formulating strategic landscape policies, goals, and objectives, which are translated into tactical plans and actions taken at the stand scale (Gunn 1996; Andison 2003). The critical management challenge inherent in this process is making sure that the sum of all of the operational decisions will meet the long-term landscape objectives. The most common approach used to project the impact of different operational decisions on the landscape patterns over time (optimization models; Andison 2003) suffers from several important limitations including model complexity and loss of transparency (Weintraub and Davis 1996; Yoshimoto 2001), poorly quantified objectives (Gilmore 1997), subjective weighting of optimization criteria (Weintraub and Davis 1996), and dealing poorly with uncertainty (Gunn 1996). Our study explores the use of an alternative approach called "scenario modeling" that overcomes many of these shortcomings (Yamasaki et al. 2001) including incorporation of uncertainties, maintaining transparency (given a change in a tested management strategy, one clearly sees a range of possible forest responses), and increasing the potential involvement of stakeholders.

Managers must continually assess what level of uncertainty is acceptable before they implement plans that have long-term consequences. Thus, it is vital to have the most complete understanding of model limitations as possible. It is critical that both the fine-scale and the landscape-scale models have been as fully tested and evaluated as possible before comparing them with an approach like this. This gives managers suitable confidence in the basic model per-

formance. Then, managers can evaluate whether an initial difference of 10%–20% between the two models in the forecasted presence on the landscape represents too high a level of model uncertainty. The value of this approach is that it gives important additional information to managers regarding the risks involved in designing and testing management strategies. It has been argued that scenario planning has suffered from requiring high technological expertise, time, and resources that are out of the reach of many agencies (Andison 2003), but the approach outlined in our study is more in accord with Peters et al. (2004) in illustrating a feasible approach to scenario modeling that is relatively accessible and affordable.

Conclusion

Spatial interactions among trees within a stand add important details that impact forecasts of spatial heterogeneity of species composition at the landscape scale. In the absence of adequate long-term data from multispecies stands on a range of landtypes, we can improve our confidence in such forecasts by exploring the different ways that forest dynamics models designed for different scales and based on complimentary approaches capture spatial and temporal heterogeneity of tree species. In this study, we made use of two recognized types of models of forest dynamics that differ in their structure and the scale at which they are applied that have been validated for these forests. We found consistencies in model forecasts such as generally similar rank patterns of presence that increase our confidence in the forecasts of average landscape dynamics, but we also found key differences, such as among forecasts in the persistence of midtolerant species and understory dynamics, that illustrate the need for the inclusion of more process detail or more sophisticated methods of including variation in stand dynamics in our landscape models for certain applications. We also found that different ways of scaling the underlying data resulted in unexpected and significantly different forecasts in the effects of harvest scenarios (e.g., gaps). By making use of the strengths of different models designed to operate best at their appropriate scales, managers can explore and buttress key weaknesses of each such that forecasts of forest dynamics can be improved to meet the multiple objectives of modern forest management. Hence, multiple uses of forests should be managed by integrating both stand and landscape scales within a unified conceptual framework. The approach described in this study is practical, is accessible to forest managers, does not incur undue computational costs or model complexity, and, by carefully comparing different models, offers an alternative approach for error and model uncertainty analysis in the absence of long-term, broad-scale empirical data.

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